NEW YORK ENTOMOLOGICAL SOCIETY
LXXXVI(3), 1978, pp. 132–136

FORAGING TRAILS OF LEAF-CUTTING ANTS

Harold G. Fowler

Abstract.—Fowler, Harold G., Department of Entomology & Economic Zoology, Rutgers—The State University, New Brunswick, New Jersey 80903 U.S.A.—Leaf-cutters construct and maintain well defined foraging trails, which can be easily quantified. To examine the relationship between ant activity and trail measurements, colonies of eight species of *Atta* and *Acromyrmex* were examined. A significant correlation was found between leaf inputs per day and colony trail measurements (trail development). Also, the number of ants returning unladen was also correlated with the degree of trail development. Unladen ants have been postulated to comprise the trail maintenance force. However, no correlation was found between trail development and the proportion of ants returning unladen. This suggests that no predictions can be formulated concerning the proportion of foragers that must be diverted to trail maintenance.

Received for publication March 29, 1978.

Introduction

The Gardening Ants (tribe Attini) are among the dominant invertebrates of the Neotropics (Wheeler 1907). The higher attine genera *Atta* and *Acromyrmex* comprise the true leaf-cutting ants, harvesting vegetation to use as substrate in the cultivation of fungus. All species of *Atta* and many species of *Acromyrmex* construct and maintain conspicuous foraging trails, over which harvested vegetation is transported to the nest. Other species of *Acromyrmex* and the lesser genera of attines exhibit a much smaller degree of trail construction. Apparently all members of the Attini employ trail pheromones (Robinson et al. 1974) to recruit workers to suitable resource patches. Carroll and Janzen (1973) postulated that physically defined foraging trails would be expected for ants exploiting predictable resources, while pheromone trails would be employed to exploit low permanence resources. However, the integration of physical and chemical trails in the foraging strategies of leaf-cutting ants has not been eludicated.

The colony cost of foraging trail maintenance has been treated by Lugo et al. (1973) in a study of the energetics of an *Atta colombica* colony. These authors hypothesized that the trail maintenance force consisted of those ants which return to the nest unladen, and they further hypothesized that the size of the nest maintenance force ultimately determines colony size. Species characterized by a reduced or non-existant foraging trail system

were ignored by these authors. This report addresses this omission by testing an extension of the hypothesis of Lugo et al.: if those ants returning unladen constitute the trail maintenance force, the number of returning unladen workers should increase with increasing foraging trail development. This report also addresses an implicit assumption of the hypothesis by Carroll and Janzen (1973) that a high degree of physical trail development indicates a high predictability of resources and consequently should provide for a high input of resources into the colony, while the opposite should be expected for those species employing a reduced degree of trail development.

Methods

Field observations were conducted in a mixed hardwood forest near Asuncion, Paraguay, and in a *Copernica* sp. palm savanna in the lower Chaco, 40 km west of Asuncion, in January 1975. Mature colonies of leaf-cutting ants examined were two each of *Acromyrmex rugosus rugosus*, *Acromyrmex landolti fracticornis*, and *Acromyrmex lundi pubescens*, and one each of *Atta sexdens rubropilosa*, *Atta vollenweideri*, *Acromyrmex crassispinus*, *Acromyrmex laticeps* and *Acromyrmex heyeri*. The degree of trail development by each colony studied was quantified by measuring the length of all discernible physical trails (m), multiplying this value by the mean trail width (m), and then dividing by 100 to provide a 'trail index.' Mean trail width was calculated separately for each trail from measurements taken at 10 equidistant points along the trail from proximal to distal ends.

Foraging was monitored by hourly counts of the number of laden and unladen ants returning to the colony per 3 minutes. Census periods ranged from 24 to 240 hr. Due to rhythmic foraging cycles exhibited by the ants, foraging was monitored throughout the day. A 'trail maintenance ratio' was calculated using the index of Lugo et al. (1973), which is the ratio of unladen to laden ants.

Results and Discussion

With the exception of *A. lundi pubescens*, species of *Atta* exhibited a greater degree of trail development than species of *Acromyrmex* (Table 1). Moreover, a significant correlation was found between trail development (trail index) and the input of substrate into the nest (number of incoming laden/day) ($r = 0.940$, $P < 0.01$), clearly suggesting the adaptive value of foraging trail development in resource exploitation. If trails develop in response to large or extremely profitable resource patches (Carroll and Janzen 1973), then trail development would allow for the exploitation of distant, predictable patches, and permit the ants to conservatively manage the resources within the foraging territory of the colony (Cherrett 1968; Rockwood 1976). At the other end of the scale, *A. rugosus rugosus*, which forages on

Table 1. Physical trail development and 'maintenance' indices of some mature, healthy colonies of Paraguayan leaf-cutting ants.

Species	Hours observed	No. of trails	Trail index[a]	Incoming ants/day[b] laden	Incoming ants/day[b] unladen	'Maintenance' index[c]
Atta						
sexdens	240	9	15.295	62,840	49,978	0.795
vollenweideri	24	14	9.450	27,552	11,418	0.414
Acromyrmex						
crassispinus	240	3	0.980	1,735	4,107	2.367
heyeri	24	4	0.780	3,228	2,089	0.647
laticeps	240	1	0.744	213	38	0.178
landolti	240	1	0.045	157	75	0.478
	240	1	0.060	151	101	0.669
lundi	24	5	2.950	4,673	3,342	0.715
	24	4	4.025	3,312	2,199	0.664
rugosus	240	1	0.092	58	18	0.310
	240	1	0.176	93	32	0.344

[a] Trail index = total length of trails × mean trail width/100.

[b] From hourly 3 min counts. To obtain an estimate of the total incoming number of ants/day, multiply these figures by 20.

[c] Maintenance index = ratio of unladen to laden ants, after Lugo et al. (1973).

leaf and flower fall (unpublished), possesses only short trunk trails to direct foragers toward likely sites, much as in *Pogonomyrmex* spp. (Hölldobler 1976). Likewise, *A. landolti fracticornis*, a grass cutter, does not construct extensive foraging trails, but rather utilizes the discontinuities of the clonal growth pattern of the grass to reach cutting sites.

The construction and maintenance of foraging trails would present the colony with an added contingency to be met in order to maximize fitness (Wilson 1968). To examine trail maintenance further, an examination of Table 1 reveals a strong correlation between the number of ants returning unladen and the trail index ($r = 0.918$, $P < 0.01$). However, do the proportion of ants returning unladen constitute the trail maintenance force?, and if so, should we expect that as trail development increases the proportion of workers diverted to maintenance should also increase? This was disproven by a weak correlation ($r = 0.004$) between the trail index and the maintenance index. Thus, we may assume that the total number of ants that might be diverted to trail maintenance increases linearly with trail development, but the proportion available for maintenance does not.

Although these results are based on one or two colonies per species, the results indicate that there is a linear relationship between trail development and ant activity, even across generic lines. Obviously, the proportion of

ants returning unladen cannot be used as a gauge of trail maintenance. It is possible that to maximize input of energy into the nest, there may be an optimum ratio of maintenance workers to foraging workers. Likewise, there is probably a maximum distance after which it is energetically too costly to forage, due to maintenance and travel time, and thus might explain the linear relationships found here. Exactly why so many ants return unladen is unclear, but it is improbable that all of these comprise the trail maintenance force. Littledyke and Cherrett (1976) have shown that workers of *Atta cephalotes* and *Acromyrmex octospinosus* directly imbibe plant sap, and a large portion of the ants returning unladen to the nest may be transporting plant sap. Also, as older workers tend to do the foraging in many species of ants (Rosengren 1971), a portion of those ants seen unladen on the trail may be young foragers just learning their way around the colony's foraging territory. During this study, maintenance indices on the order reported by Lugo et al. (1973) were not observed, but it may be that tropical species must divert more workers into 'maintenance' than their subtropical counterparts.

Acknowledgments

This work was conducted while I was employed at the Instituto de Ciencias Basicas, Universidad Nacional de Asuncion. Support was supplied in part by the Instituto de Ciencias Basicas, the Paraguayan Ministry of Agriculture, U.S. Peace Corps/Paraguay, UNESCO, the British Ministry of Overseas Development, and the New Jersey Experiment Station.

Literature Cited

Carroll, C. R., and D. H. Janzen. 1973. Ecology of foraging by ants. Ann. Rev. Ecol. Syst. 4:231–257.

Cherrett, J. M. 1968. The foraging behavior of *Atta cephalotes* L. (Hymenoptera: Formicidae). I. Foraging patterns and plant species attacked in tropical rain forests. J. Anim. Ecol. 37:397–403.

Holldobler, B. 1976. Recruitment behavior, home range orientation and territorality in harvester ants, *Pogonomyrmex*. Behav. Ecol. Sociobiol. 1:3–44.

Littledyke, M., and J. M. Cherrett. 1976. Direct ingestion of plant sap from leaves cut by the leaf-cutting ants *Atta cephalotes* (L.) and *Acromyrmex octospinosus* (Reich) (Formicidae: Attini). Bull. ent. Res. 66:205–217.

Lugo, A. E., E. G. Farnsworth, D. G. Pool, P. Jerez, and G. Kaufman. 1973. The impact of the leaf-cutter ant *Atta colombica* on the energy flow of a tropical rain forest. Ecology 54:1292–1306.

Robinson, S. W., J. C. Moser, M. S. Blum, and E. Amante. 1974. Laboratory investigations on the trail-following responses of four species of leaf cutting ants with notes on the specificity of trail pheromone of *Atta texana* (Buckley) Insectes Soc. 21:87–94.

Rockwood, L. L. 1976. Plant selection and foraging patterns in two species of leaf-cutting ants (*Atta*). Ecology 57:48–61.

Rosengren, R. 1971. Route fidelity, visual memory and recruitment behavior in foraging wood ants of the genus *Formica*. Acta. Zool. Fennica 133:1–106.

Wheeler, W. M. 1907. The fungus-growing ants of North America. Bull. Amer. Mus. Nat. Hist. 23:669–807.

Wilson, E. O. 1968. The ergonomics of caste in the social insects. Am. Natur. 102:41–66.